# A NEW FOSSIL STORK (AVES, CICONIIDAE) FROM THE LATE TERTIARY OF LANGEBAANWEG, SOUTH AFRICA

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(With 3 figures and 4 tables)

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ABSTRACT

A new species of stork, *Ciconia kahli*, from the early Pliocene Varswater Formation, Cape Province, South Africa, is described on the basis of a partial associated skeleton and three other referred specimens. This species has the greatest similarity to the living white stork, *Ciconia ciconia*, but also resembles the saddlebill stork, *Ephippiorhynchus senegalensis*, and black-necked stork, *E. asiaticus*, in certain characters. It is nevertheless very distinctive and probably represents an extinct lineage within the Ciconiidae.

CONTENTS



## INTRODUCTION

The early Pliocene (*c.* 5 Ma) Varswater Formation at Langebaanweg, approximately 110 km north-north-west of Cape Town, has yielded a great number and variety of fossils (Hendey 1981*a*, 1981*b*). In a preliminary report on the avian remains from this site Rich (1980) listed a minimum of 61 taxa. Further research on the collection has raised the number of species to 81. Simpson (1971, 1975, 1979) studied the penguin material, which is now being re-examined by Olson (1983, in prep.). Olson (1984) has also described a new species of the ciconiiform family Scopidae, *Scopus xenopus*, and has studied the Procellariiformes (1985*a*) and the ciconiiform family Plataleidae (1985*b*). Rich & Haarhoff (1985) have described a new species of the family Coliidae, *Colius hendeyi*. The associated stork remains described in this paper are from the Quartzose Sand Member (QSM), the lower of the two highly fossiliferous units of the Varswater Formation. This unit accumulated behind a sand-bar in and adjacent to the estuary of the Berg River, which now has a more northerly course. The QSM contains fluviatile, estuarine, floodplain, marsh, tidal mudflat,



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and pond facies (Hendey 1976). The partial stork skeleton, SAM–PQ–L22164, was found *in situ*, in the floodplain deposits (QSM 1) of the Quartzose Sand Member. Three other bones of uncertain provenance have been referred to the same species.

Kahl's (1972) classification of living storks is followed here (Table 1), although it requires revision (see p. 310). Comparisons with living species indicate that, on the basis of the premaxilla and mandible, the fossil stork belongs to the tribe Ciconiini. The postcranial material is sufficiently different from all the living species and all known fossil species to warrant assignment to a new species. The new fossil stork does bear certain resemblances to *Ciconia ciconia* and to a lesser extent to *Ephippiorhynchus senegalensis* and *E. asiaticus*.

The material described is housed in the Department of Cenozoic Palaeontology, South African Museum. Catalogue numbers of fossil material are prefixed SAM–PQ, with the additional prefix L indicating material from Lange-

TABLE 1

Classification of the Ciconiidae according to Kahl (1972).

| | |
|---|---|
| **Family Ciconiidae** | |
| Tribe Mycteriini | |
| *Mycteria americana* Linnaeus | American wood stork |
| *Mycteria cinerea* (Raffles) | milky stork |
| *Mycteria ibis* (Linnaeus) | yellowbilled stork |
| *Mycteria leucocephala* (Pennant) | painted stork |
| *Anastomus oscitans* (Boddaert) | Asian openbill stork |
| *Anastomus lamelligerus* Temminck | African openbill stork |
| *A. l. lamelligerus* Temminck | |
| *A. l. madagascariensis* Milne Edwards | |
| Tribe Ciconiini | |
| *Ciconia nigra* (Linnaeus) | black stork |
| *Ciconia abdimii* Lichtenstein | Abdim's stork |
| *Ciconia episcopus* (Boddaert) | woollynecked stork |
| *C. e. episcopus* (Boddaert) | |
| *C. e. microscelis* G. R. Gray | |
| *C. e. stormi* (Blasius)* | |
| *Ciconia maguari* (Gmelin) | maguari stork |
| *Ciconia ciconia* (Linnaeus) | white stork |
| *C. c. ciconia* (Linnaeus) | |
| *C. c. asiatica* Severtzov | |
| *C. c. boyciana* Swinhoe* | |
| Tribe Leptoptilini | |
| *Ephippiorhynchus asiaticus* (Latham) | blacknecked stork |
| *E. a. asiaticus* (Latham) | |
| *E. a. australis* (Shaw) | |
| *Ephippiorhynchus senegalensis* (Shaw) | saddlebill stork |
| *Jabiru mycteria* (Lichtenstein) | jabiru stork |
| *Leptoptilos javanicus* (Horsfield) | lesser adjutant stork |
| *Leptoptilos dubius* (Gmelin) | greater adjutant stork |
| *Leptoptilos crumeniferus* (Lesson) | marabou stork |

*Possibly has attained specific status; further study needed.

baanweg. Modern comparative material in the South African Museum is distinguished by the prefix SAM–ZO.

Institutional abbreviations used in the text are as follows:

| | |
|---|---|
| AMNH | American Museum of Natural History, New York. |
| AM–S | Australian Museum, Sydney. |
| ANWC | Australian National Wildlife Collection, Canberra, Australia (CSIRO). |
| BMNH | British Museum (Natural History), London. |
| LACM | Natural History Museum of Los Angeles County, California. |
| NMV | National Museum of Victoria, Australia. |
| OT–B | Otago Museum, Dunedin, New Zealand. |
| SAM | South African Museum, Cape Town. |
| TM | Transvaal Museum, Pretoria. |
| UCMP | University of California, Museum of Paleontology, Berkeley. |

Most measurements (in mm) were taken following Von den Driesch (1976) and Olson (1985*b*). Anatomical terminology follows that of Howard (1929).

*Comparative material examined*

*Mycteria americana*, SAM–ZO57920; *M. leucocephala*, BMNH 396A, BMNH 396B; *M. ibis*, AM–S 1235; *Anastomus lamelligerus*, TM 33382, AMNH 5292; *Ciconia nigra*, SAM–ZO56944, OT–B76:1; *C. abdimii*, TM 33336; *C. episcopus*, TM 33391; *C. maguari*, AM–S 551; *C. ciconia*, SAM–ZO56181, SAM–ZO57363, SAM–ZO57471, AM–S 1126; *Ephippiorhynchus asiaticus*, BMNH 955B, ANWC 108, ANWC 686, ANWC 4139, ANWC 1508, NMV–B6753; *E. senegalensis*, LACM 90275, AMNH 2903; *Leptoptilos dubius*, NMV–B11426, NMV–R2203, NMV–W5083; *L. crumeniferus*, TM 33412; *L. javanicus*, NMV–B736, AMNH 5059; *Jabiru mycteria*, AMNH 2659, UCMP 133932.

## SYSTEMATICS

### Family **Ciconiidae** Gray, 1840

The fossil specimens can be referred to the Ciconiidae on the basis of the following characters: (1) sternum excavated on anterior carinal margin; (2) last thoracic vertebra not fused to synsacrum; (3) synsacrum, cranial view, prezygapophysis not joined to diapophysis at posterior edge; (4) scapular facet of coracoid deep and well rounded; (5) carpal tuberosity of ulna pointed, with ligamental attachment on caudal surface; (6) intercotylar prominence on tarsometatarsus rises well above cotylae, which are more or less of equal height; and (7) trochleae II and IV rather flattened anteriorly, not rounded. Characters 1, 4, 5, 6, and 7 separate the Ciconiidae from the Scopidae, Ardeidae and Plataleidae, character 2 from the Scopidae, and character 3 from the Ardeidae and Plataleidae.

## Genus *Ciconia* Brisson, 1760

The fossil species described below is referable to the genus *Ciconia* by having the combination of: (1) tips of maxilla and mandible straight; (2) anterior carinal margin of sternum unperforated; (3) coracoid with a ridge between head and midpoint of shaft in ventral view; (4) deep depression between the proximal articulating surface of the tarsometatarsus and the hypotarsus; and (5) lack of significantly pneumatic postcranial elements.

Characters 1–5 distinguish the genus *Ciconia* from the other five Recent genera of Kahl (1972) and therefore the following putative extinct species within those genera: *Mycteria wetmorei* Howard, 1935; *Leptoptilos falconeri* (Davies, 1880) (Lydekker 1884; Harrison 1974); *L. siwalikensis* Harrison, 1974; *L. richae* (Harrison, 1974); *L. titan* Wetmore, 1940; *L. pliocenicus* Zubareva, 1948; *Leptoptilos* sp. Hill & Walker, 1979; *Ephippiorhynchus pakistanensis* Harrison & Walker, 1982.

The fossils from Langebaanweg were also compared with and found to be distinct from the following extinct genera: *Palaeoephippiorhynchus dietrichi* Lambrecht, 1930; *Grallavis edwardsi* (Lydekker, 1891) (Lambrecht 1933; Cheneval 1984); *'Propelargus' olseni* Brodkorb, 1963 (requires revision, Cheneval pers. comm.); *'Dissouroides' milleri* Short, 1966 (requires revision, Olson pers. comm.); *Cryptociconia indica* Harrison, 1974; *Pelargosteon tothi* Kretzoi, 1962; *'Prociconia' lydekkeri* Ameghino, 1891 (requires revision, Olson pers. comm.). *Ciconiopsis antarctica* Ameghino, 1899, was not studied by the author but, since it is from the early Oligocene of Argentina, it seems unlikely that the fossils from Langebaanweg should be assigned to this genus. Also, according to Olson (1986), it requires restudy before it can be accepted as a stork.

### ***Ciconia kahli*** sp. nov.

Figs 1–3

*Material*

*Holotype*. SAM–PQ–L22164, partial associated skeleton consisting of the following elements: fragment of premaxilla (length 53,7 mm), mandibular symphysis (length 80,7 mm) plus associated fragments; part of sternal manubrium and coracoidal sulcus; complete furcular process plus fragmented pieces; complete left proximal and incomplete right proximal scapulae; incomplete left and right coracoids; incomplete left distal humerus; fragments of head, shaft, and distal end of right humerus; almost complete right ulna; external cotyla and crushed fragments of shaft of left ulna; complete right radius (slightly damaged proximal end); right scapholunar; right cuneiform; right carpometacarpus; right phalanx 1 and 2 of major alar digit; incomplete right femur; incomplete distal end of left tibiotarsus and shaft; incomplete right fibula; incomplete left tarsometatarsus (lacks distal end); pes—incomplete ungual phalanx, possibly of digit 3; first and second thoracic vertebrae; eleventh and twelfth cervical vertebrae (pathological), plus numerous vertebral fragments.

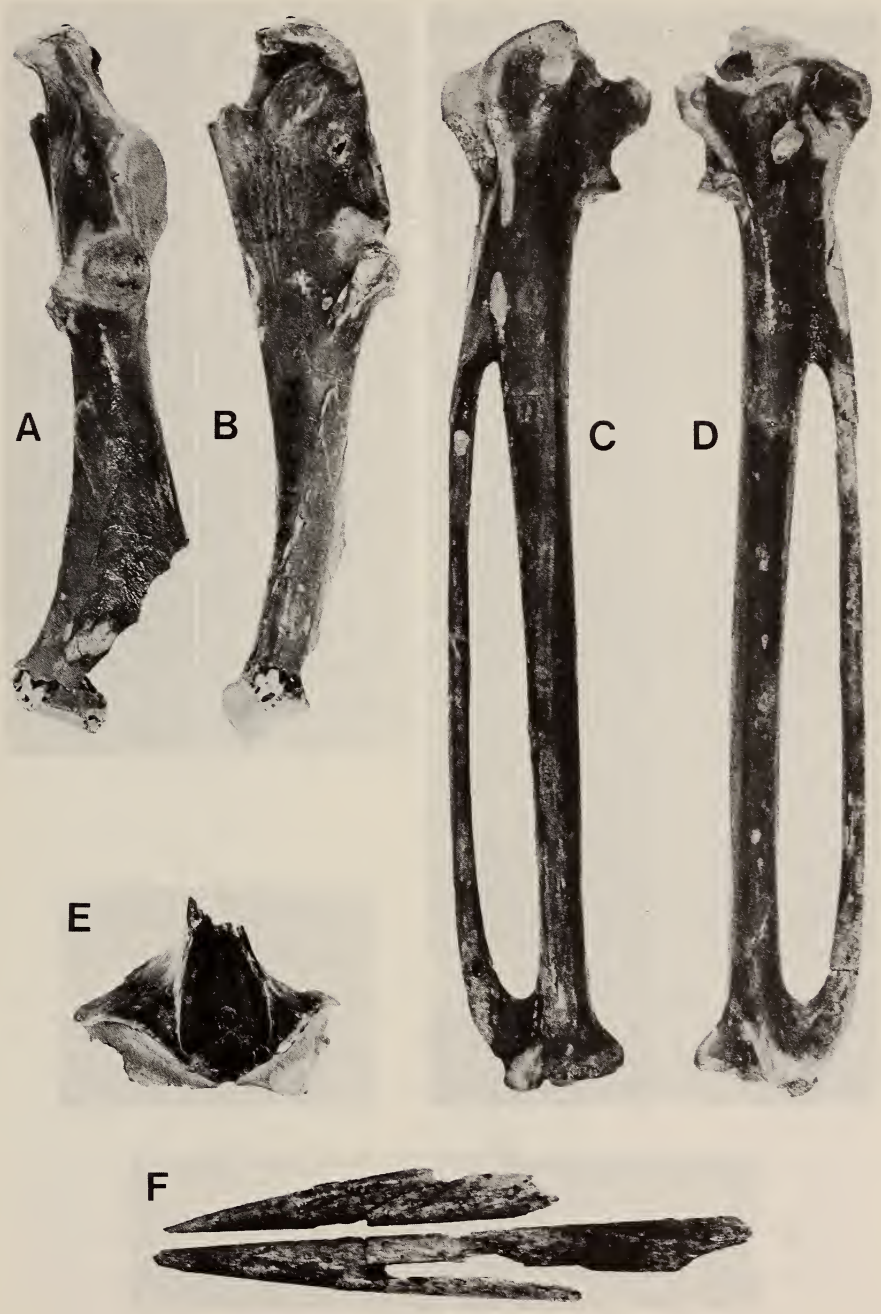


Fig. 1. *Ciconia kahli* sp. nov., holotype, SAM–PQ–L22164. A–B. Coracoid. C–D. Carpometacarpus. E. Sternum. F. Maxilla and mandible. All × 1.

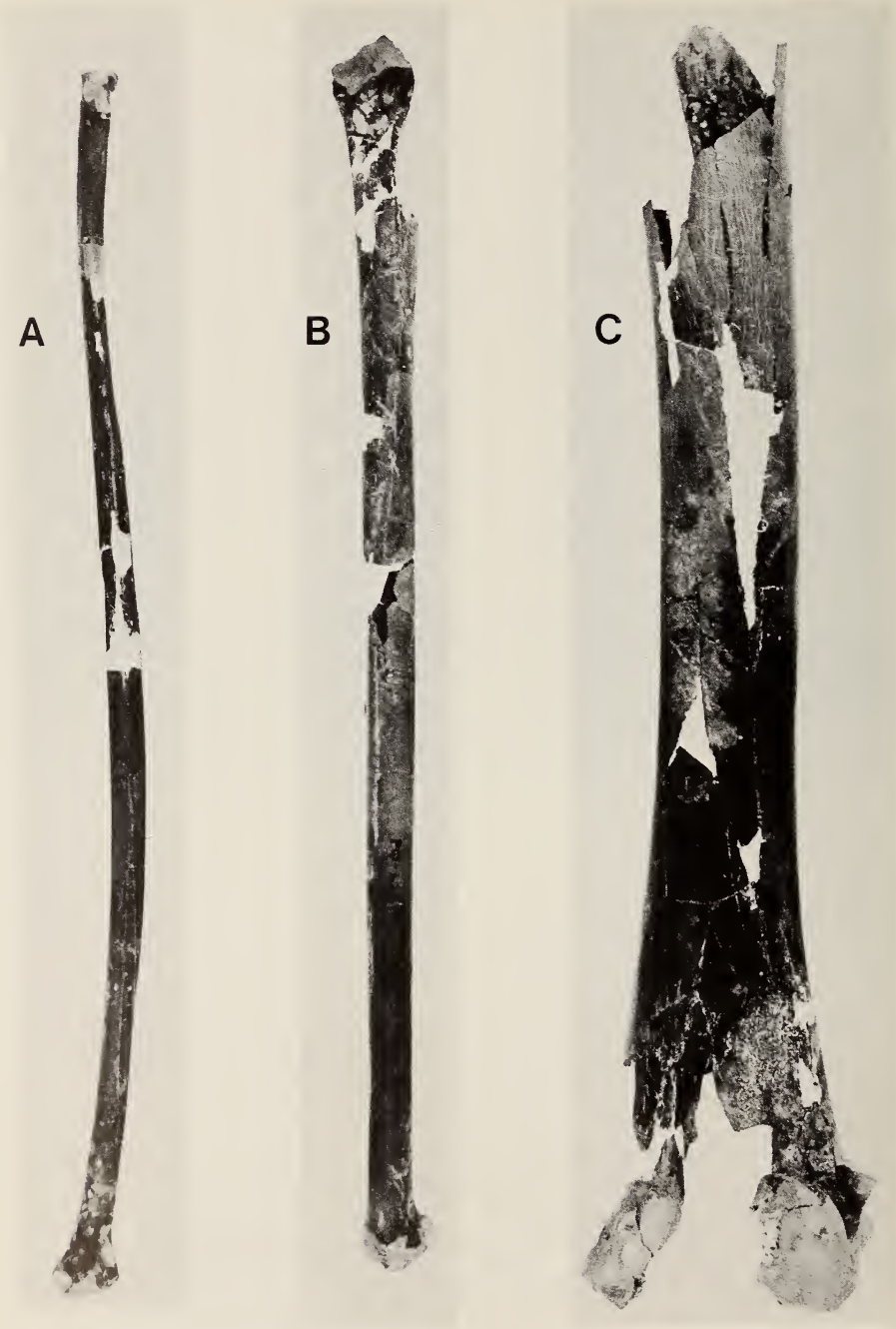


Fig. 2. *Ciconia kahli* sp. nov., holotype, SAM–PQ–L22164. A. Radius. B. Ulna. C. Humerus. D. Proximal end of humerus. E. Humerus (proximal view). F. Distal end of tibiotarsus (internal view). G. Femur (posterior view). H. Femur (internal view). I. Tibiotarsus. A–B. × 0,5. C–H. × 1. I. × 0,6.

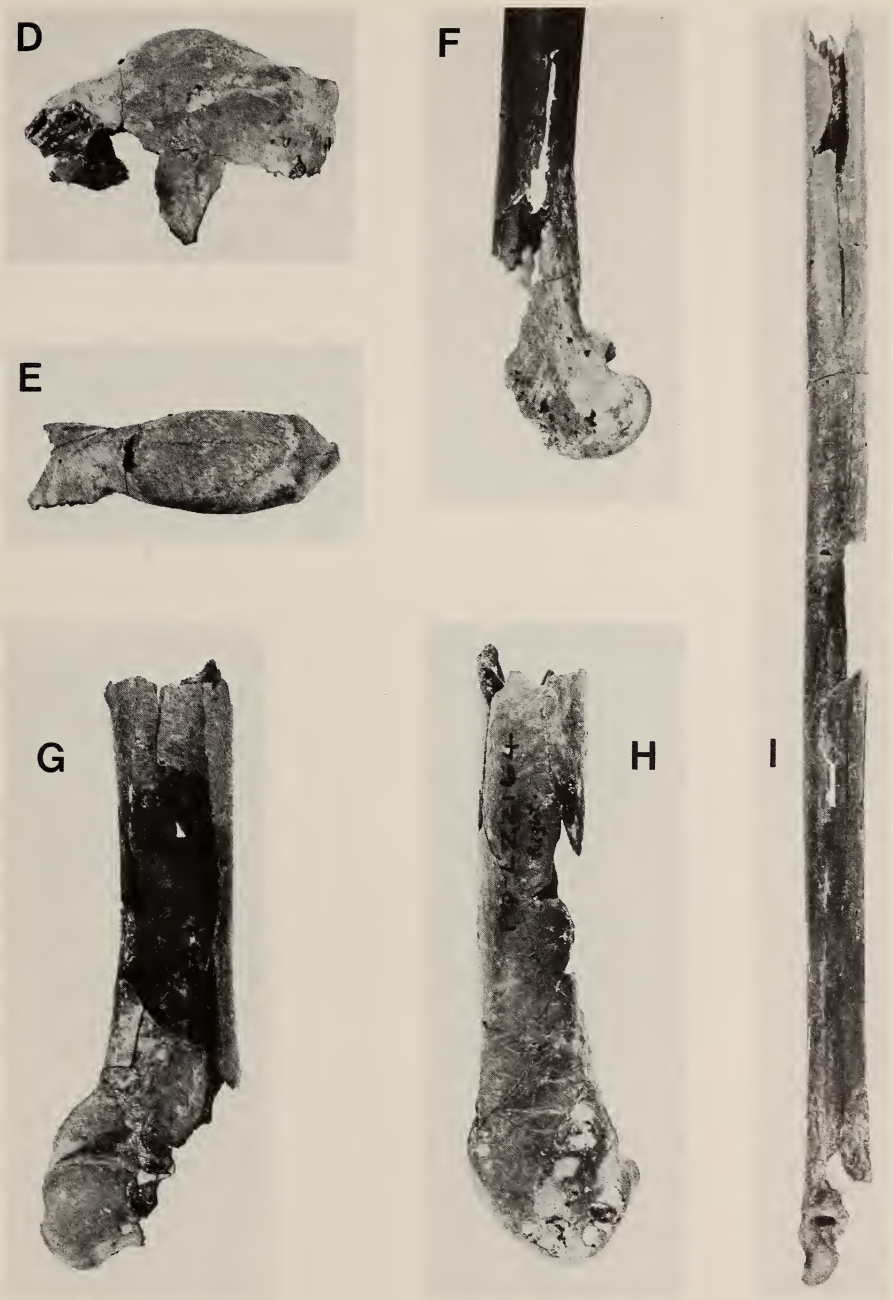


Fig. 2 (*contd*)

*Paratypes*. SAM–PQ–L41955, synsacrum lacking a few caudal vertebrae. SAM–PQ–L42157, right ulna lacking proximal end. SAM–PQ–L–6508, complete distal end of right tarsometatarsus (Fig. 3). Including the holotype, the minimum number of individuals is two.

*Measurements of holotype* (in mm)

Humerus: actual length, 180,0; estimated greatest length, 274,0; estimated distal width, 41,2; smallest width of shaft, 19,1. Ulna: actual length of proximal portion, 133,4; actual length of distal portion, 183,0; estimated greatest length, 320,0; greatest diagonal of distal end, 20,9; smallest width of shaft, 9,5. Radius: greatest length, 304,0; least and greatest diameter of shaft at midpoint, $5{,}1 \times 8{,}7$; greatest distal diameter, 18,4. Carpometacarpus: greatest length, 144,3; depth through process of metacarpal 1, 29,0; greatest proximal width through trochleae, 12,6; width and depth of major metacarpal at midpoint, $9{,}7 \times 6{,}9$; greatest distal diameter, 16,3. Coracoid: medial length, 93,4; estimated greatest length, 103,0; greatest depth of sternal facet, 12,6. Sternum: greatest width of excavation on anterior carinal margin, 12,0; greatest breadth of coracoidal sulcus, 14,1. Scapula: greatest cranial diagonal, 26,6. Femur: actual length, 32,5; estimated greatest length, 117,9; approximate shaft width and depth, $15{,}2 \times 15{,}4$. Tibiotarsus: actual length, 267,7; estimated greatest length, 348,0; width and depth of shaft at approximate midpoint, $14{,}6 \times 11{,}2$; depth of anterior internal condyle, 13,8; length of supratendinal bridge, 6,3. Fibula: actual length, 51,4; estimated greatest length, 230,0. Tarsometatarsus: actual length, 292,1; estimated greatest length, 321,7; proximal width, 22,5; approximate width and depth of shaft at approximate midpoint, $9{,}7 \times 9{,}4$.

*Measurements of paratypes* (in mm)

Synsacrum, SAM–PQ–L41955: actual length, 96,1; depth at midpoint of second synsacral thoracic vertebra, 36,4; width of first synsacral thoracic vertebra at midpoint, 7,4. Ulna, SAM–PQ–L42157: actual length, 158,6; greatest diagonal of distal end, 20,9. Tarsometatarsus, SAM–PQ–L6508: distal width, 24,5; width and depth of middle trochlea, $7{,}9 \times 11{,}7$.

*Diagnosis*

Larger than all five extant species of *Ciconia* (Table 2) and the extinct species *Ciconia minor* Harrison, 1980, *Ciconia sarmatica* Grigorescu & Kessler, 1977, and *Ciconia nana* (De Vis, 1888) (Rich & Van Tets 1982). Also larger than *Ciconia* sp. Harrison, 1980, and *Ciconia* sp. Ono, 1984. *Ciconia* sp. Stehlin, 1923, is juvenile and was not considered. Smaller than *Ciconia gaudryi* Lambrecht, 1933. Within size range (Table 3) of the extinct species *Ciconia maltha* Miller, 1910, but morphologically distinct as follows: sternum—excavation on anterior carinal margin shallower and wider; coracoid—internal view, less inflated below depression beneath brachial tuberosity and brachial tuberosity less erect; humerus—shaft more robust (see also unique features below);

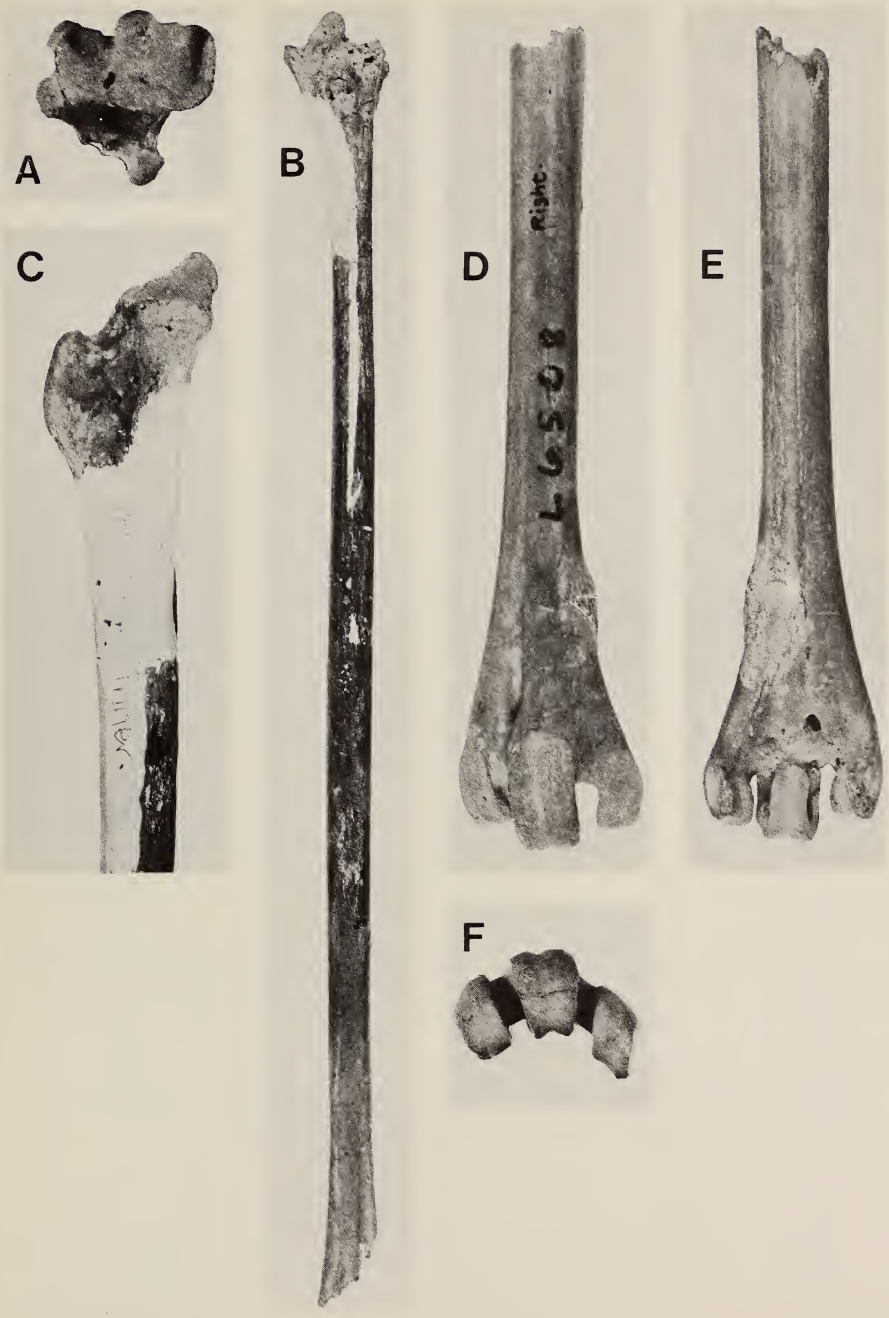


Fig. 3. *Ciconia kahli* sp. nov. A–C. Holotype, SAM–PQ–L22164. Tarsometatarsus. A. Proximal view. B. Anterior view. C. Internal view. D–F. Paratype, SAM–PQ–L6508. Tarsometatarsus. D. Anterior view. E. Posterior view. F. Distal view. A, C–F. × 1. B. × 0,6.

TABLE 2

Length measurements (mm) of major elements of *Ciconia kahli* sp. nov. compared with extant species of *Ciconia*.

| | *C. kahli* (n = 1) | *C. nigra* (n = 2) | *C. abdimii* (n = 1) | *C. episcopus* (n = 1) | *C. maguari* (n = 1) | *C. ciconia* (n = 4) |
|---|---|---|---|---|---|---|
| Coracoid | 103* | 77,5–85,5 | 63,5 | 66,4 | 97,9 | 80,5–90,9 |
| Humerus | 274* | 191,4–197,1 | 151,7 | 158,1 | 223,5 | 196,8–213,8 |
| Ulna | 320* | 218,4–230,9 | 174,0 | 185,7 | 265,4 | 227,1–253,0 |
| Radius | 304 | 209,4–220,0 | 166,3 | 179,0 | 254,3 | 216,1–242,8 |
| Carpometacarpus | 144,3 | 110,7–113,5 | 84,0 | 85,4 | 119,5 | 107,7–114,6 |
| Femur | 117,9* | 94,5–94,8 | 71,6 | 73,9 | 113,0 | 90,1–110,7 |
| Tibiotarsus | 348* | 239,1–246,6 | 177,6 | 202,6 | 311,4 | 238,2–260,8 |
| Tarsometatarsus | 321,7* | 192,4–200,1 | 133,5 | 150,2 | 272,4 | 198,1–225,1 |

* = estimated

tarsometatarsus—intercotylar prominence narrower, in distal view trochleae less arched and trochlea III less raised and rounded in external view in *C. kahli*.

*Ciconia kahli* differs morphologically from the extant species of *Ciconia* as follows: sternum—expanded coracoidal sulcus; coracoid—neck proportionally longer; radius—shaft less curved; carpometacarpus—inner carpal trochlea, internal view, flattened anteriorly; tibiotarsus—internal ligamental prominence placed further away from internal margin; tarsometatarsus—depression between hypotarsus and proximal articulating surface deeper in *C. kahli*.

Certain features of the humerus of *C. kahli* are different from all species of Ciconiidae studied for this report: (1) head, palmar view, relatively flattened, sloping gradually toward external side; (2) proximal view, head broader near external tuberosity; (3) capital groove shallow; (4) groove between ectepicondylar prominence and external condyle deep.

*Distribution*

Early Pliocene Varswater Formation (Quartzose Sand Member Unit I and possibly Pelletal Phosphorite Member bed 3aS) at Langebaanweg, southwestern Cape Province, South Africa.

*Etymology*

This species is named in honour of Dr M. Philip Kahl, who has done so much work on the Recent genera of the family Ciconiidae.

*Remarks*

Although *Ciconia kahli* has the greatest similarity to *C. ciconia*, it shares the following characters with *Ephippiorhynchus*: (1) twelfth cervical vertebra not longitudinally compressed; (2) first and second thoracic vertebrae with hypapophyses; (3) ulna, in palmar view, flattened immediately below the proximal radial depression; (4) carpometacarpus, in internal view, with a deep depression between metacarpal I and the pisiform process; (5) internal condyle of tibiotarsus,

TABLE 3

Comparative measurements (mm) for fossil species of *Ciconia* and *Ciconia kahli* sp. nov.

| | | *Ciconia* sp.[1] | *Ciconia minor*[2] | *Ciconia* sp.[2] | *Ciconia gaudryi*[3] | *Ciconia nana*[4] (n = 2) | *Ciconia maltha*[5] | *Ciconia sarmatica*[6] | *Ciconia kahli*[4] |
|---|---|---|---|---|---|---|---|---|---|
| | | Japan | Kenya | Kenya | Greece | Australia | California Florida Oregon Idaho | Romania | South Africa |
| Scapula | bp | | | | | | 26,4–27,0 | | 26,6 |
| Humerus | gl | | | | 310 | | 250–280 | | 274* |
| Ulna | gl | | | | | | 318–338 | | 320* |
| Carpometacarpus | gl | | | | | | 129,5–151,5 | 120–125 | 144,3 |
| | bp | | | size of *C. ciconia* | | | | 23,6 | |
| Carocoid | gl | | | | | | 82,4–101,2 | | 103* |
| Femur | gl | | | | | | 105,2–123,2 | | 117,9* |
| | bd | | 2/3 size of *C. ciconia* | | | | | | |
| Tibiotarsus | lsb | | | | | 4,6–4,7 | | | 6,3 |
| | gl | | | | | | 315–363 | | 348* |
| | daic | | | | | 10,6–11,5 | | | 13,8 |
| | bd | | | | | 14,6–16,0 | 18,0–21,5 | | |
| Tarsometatarsus | gl | 200* | | | | | 259,8–320 | | 321,7* |
| | bp | | | | | | 20–24,5 | | 22,5 |
| | bd | | | | | | 23–28 | | 24,5 |

* = estimated; bp = proximal breadth; gl = greatest length; bd = distal breadth; lsb = length of supratendinal bridge; daic = depth of anterior internal condyle. References: 1. Ono 1984. 2. Harrison 1980. 3. Lambrecht 1933. 4. Present study. 5. Howard 1942. 6. Grigorescu & Kessler 1977.

TABLE 4

Age and distribution of all fossil and living storks studied for this report.

| | | NEARCTIC | NEO-TROPICAL | PALEARCTIC | ETHIOPIAN | ORIENTAL | AUSTRALASIAN |
|---|---|---|---|---|---|---|---|
| HISTORIC | | *Mycteria americana* | *Mycteria americana*<br>*Ciconia maguari*<br>*Jabiru mycteria* | *Ciconia nigra*<br>*Ciconia ciconia* | *Mycteria ibis*<br>*Anastomus lamelligerus*<br>*Ciconia nigra*<br>*Ciconia abdimii*<br>*Ciconia episcopus*<br>*Ciconia ciconia*<br>*Ephippiorhynchus senegalensis*<br>*Leptoptilos crumeniferus* | *Mycteria cinerea*<br>*Mycteria leucocephala*<br>*Anastomus oscitans*<br>*Ciconia episcopus*<br>*Ciconia nigra*<br>*Ciconia ciconia*<br>*Ephippiorhynchus asiaticus*<br>*Leptoptilos javanicus*<br>*Leptoptilos dubius* | *Ciconia episcopus*<br>*Ephippiorhynchus asiaticus* |
| PLEISTOCENE | LATE | *Mycteria americana*<br>*Mycteria wetmorei*<br>*Ciconia maltha* | *Ciconia maguari*<br>*Jabiru mycteria* (0,14)[1]<br>*Mycteria americana* (0,14)[1]<br>*'Prociconia' lydekkeri* | *Ciconia ciconia*<br>*Ciconia nigra*<br>*Mycteria (Ibis) ibis* | | *Mycteria (Ibis) leucocephala*<br>*Leptoptilos titan*<br>*Ciconia* sp. | *Ciconia nana* |
| | EARLY | | | *Pelargosteon tothi*<br>*Ciconia* sp. | | | |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| PLIOCENE | LATE | *Ciconia maltha* (3,4 + 0,27)[2] | | | | *Leptoptilos siwalikensis* (1,8–3,0)[3, 4]<br>*Leptoptilos falconeri* (1,8–3,0)[3, 4]<br>*Cryptociconia indica* (1,8–3,0)[3, 4] | |
| | MIDDLE | | | *Leptoptilos pliocenicus* | | | |
| | EARLY | *'Dissouroides' milleri* | | | *Ciconia kahli* sp. nov. (5,0)[5] | | *?Ephippiorhynchus (Xenorhynchus)* (4,0–4,5)[6] |
| MIOCENE | LATE | | | *Ciconia gaudryi* (9,0)[3]<br>*Leptoptilos richae*<br>*Ciconia sarmatica* (12,0)[8] | *Leptoptilos* sp. (11,5)[7] | *Ephippiorhynchus pakistanensis*<br>*Leptoptilos siwalikensis** | |
| | MIDDLE | *'Propelargus' olseni* (13,5–15,0)[9] | | | *Ciconia* sp. | | |
| | EARLY | | | *Grallavis edwardsi* | *Ciconia minor* | | |
| OLIGOCENE | EARLY | | *'Ciconiopsis' antarctica* | *Palaeoephippiorhynchus dietrichi* | | | |

Where possible, dates in million of years before present have been given in parentheses. References: 1. Campbell 1979. 2. Feduccia 1967. 3. Berggren & Van Couvering 1974. 4. Harrison (pers. comm.). 5. Hendey 1981*a*, 1981*b*. 6. Archer & Wade 1976. 7. Hill & Walker 1979. 8. Grigorescu & Kessler 1977. 9. Blackwelder 1980. *Tentatively referred specimen—Harrison & Walker 1982.

in distal view, with convex external margin; (6) depression between hypotarsus and proximal articulating surface; (7) trochleae, in distal view, form fairly flat, wide, arch; (8) similar shape of trochlea III and position of trochlea IV.

Proportional differences observed include the following: (1) *Leptoptilos* (apart from *L. javanicus*) is the only genus in which the ulna is longer than the tibiotarsus. *Ephippiorhynchus* is extreme in that the tibiotarsus is considerably longer than the ulna. In the relative length of the ulna and tibiotarsus, *C. kahli* is more similar to the *Ciconia* group and *Jabiru mycteria*. (2) *Ciconia kahli* differs from Recent storks in having the tarsometatarsus and tibiotarsus about equal in length, whereas in all other species the tibiotarsus is longer, especially so in *Leptoptilos crumeniferus*, *L. dubius*, and *Mycteria leucocephala*.

## DISCUSSION

Wood (1984) suggested from his phenetic analysis, based on major skeletal elements of the stork, that *Jabiru mycteria* be included in the genus *Ephippiorhynchus* and that *Ephippiorhynchus* should be transferred to the tribe Ciconiini. Observations in this report on the similarities between *Ciconia* and *Ephippiorhynchus* support this view. Also, on the basis of their comparisons of the genetic material, DNA, Sibley & Ahlquist (1985) place *Ciconia* and *Ephippiorhynchus* on the same branch of their phylogram. However, Cheneval (1984) found that, although the fossil stork *Grallavis edwardsi* is most closely related to *Ephippiorhynchus*, it also has some characters in common with *Leptoptilos*, so the fossil record may require some revision of Kahl's (1972) classification.

*Ciconia kahli* was a tall, fairly robust bird with shorter wings but longer legs than *Leptoptilos crumeniferus*. Its most distinctive features are in the humerus, radius, carpometacarpus, tibiotarsus and tarsometatarsus. Olson (pers. comm.) has pointed out that the greater size of *C. kahli* is paralleled by some of the Pliocene and Pleistocene species of *Leptoptilos* that were much larger than any modern species of that genus. As shown in Table 4, *Ciconia* is the most common and widespread genus of stork in Tertiary and Historic times. Just how the species of *Ciconia* are related to one another is as yet undetermined, but *Ciconia kahli* seems sufficiently distinct morphologically as not to have been ancestral to any living species and thus may represent an extinct lineage within the Ciconiidae.

Two species of stork occur today in the southern and south-western Cape Province of South Africa. They are *Ciconia c. ciconia* and *C. nigra*. Neither is common in the Langebaanweg area. *Ciconia c. ciconia* is a Palaearctic migrant, although a few pairs breed in the southern Cape. *Ciconia nigra* is a locally migratory species recorded as breeding in the eastern and southern Cape (Clancey 1980).

The inferred habitat (floodplain close to a river with marshy areas) is in keeping with that preferred by some contemporary species of the family Ciconii-

dae. Others, including *C. ciconia*, are opportunistic and take advantage of fires and burned areas. This could have been true of the Langebaanweg stork, for such conditions were also present at the time of deposition (Hendey 1981*b*).

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